FORESTS AND SCRUBLANDS OF NORTHERN FIORDLAND

J. WARDLE, J. HAYWARD, and J. HERBERT,
Forest and Range Experiment Station, New Zealand Forest Service, Rangiora

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ABSTRACT

The composition and structure of the forests and scrublands of northern Fiordland were recorded at 1,053 sample points. The vegetation at each sample point was classified into one of 16 associations using a combination of Sorensen's 'k' index of similarity, and a multi-linkage cluster analysis. The associations were related to habitat and the distribution of each was determined.

The influence of the introduced ungulates, red deer and wapiti, on the forests and scrublands was determined. Stand structure was analysed to provide information on the susceptibility of the vegetation to damage from browsing and on the history of ungulate utilisation of the vegetation. Browse indices were calculated to provide information on current ungulate utilisation of the vegetation.

INTRODUCTION

A reconnaissance of northern Fiordland was carried out during the summer of 1969-70 by staff of the Forest and Range Experiment Station. The purpose was to describe the composition, structure, and habitat of the forest and scrub associations, to determine both present and past influence of ungulates on them, and to establish a number of permanent reference points to permit measurement of future changes in the vegetation.

The area studied lies between the western shores of Lake Te Anau and the Tasman Sea. The southern boundary is the South Fiord of Lake Te Anau, the Esk Burn and Windward River catchments, and Charles Sound; the northern boundary is the Worsley and Transit River catchments (Fig. 1). The total area is *ca.* 700,000 acres of which almost two-thirds supports a forest or scrub cover.

The area is a deeply dissected upland rising to over 6,000ft altitude in places. The highest peaks are the Llawrenny peaks (6,440ft) and Castle Mountain (6,872ft) in the north, and Mt Irene (6,085ft) and Mt Lyall (6,097ft) in the south. The main mountain ranges are the result of considerable late Tertiary and Pleistocene movement on more or less north-trending faults. The main alpine fault follows along the western limits of the survey area and forms a fault-line coast. Successive ice advances in the Pleistocene have extensively modified the landscape to give deeply eroded glacial valleys, fiords, lake basins, cirques (which may be lake filled), sharpened mountain peaks, and aggraded

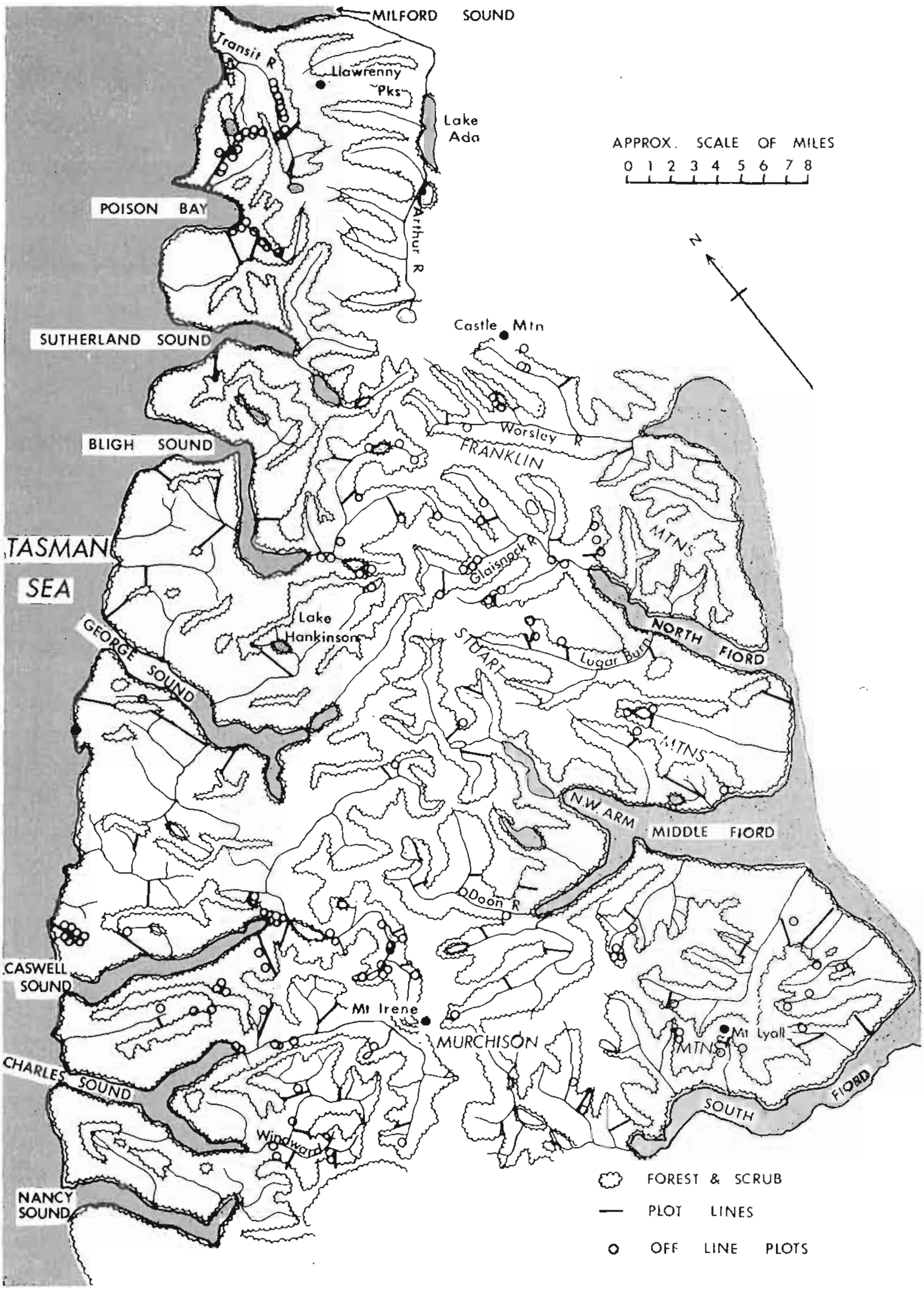

FIG. 1—Map of Survey area, northern Fiordland, showing line and plot positions.

main valleys with vast quantities of outwash alluvium (Fig. 2). The altitude of the cirque floors is commonly between 3,500ft and 4,000ft.

FIG. 2—The main Worsley valley. Note the steep valley sides and wide terraces typical of glacial sculptured landscapes.

The majority of the rocks are hard grey to pale green dioritic gneisses of the Bradshaw, Wet Jacket, Long Sound, and Milford Formations dating from the lower Permian and Cambrian. Sandstones, siltstones, and limestones occur near the shores of Lake Te Anau and are most common between the middle and south Fiords (Wood, 1960, 1962).

The major forest soils are classified as Titiraurangi (N.Z. Soil Bureau, 1968). These are thin stony loams and sandy loams developed on schist, granite, diorite, and Tertiary rocks and are of very low fertility. The Titiraurangi soils may give way to soils of the McKerrow-Resolution series under subalpine scrub. Both soils range from a fibrous peat to a peaty loam overlying a sand or sandy loam over rock.

The area lies within the zone of prevailing westerly winds. Moisture laden winds from the Tasman Sea cause heavy precipitation and frequent mist, especially in the west, when they are forced to rise over the mountain ranges. Precipitation is heavy throughout the year but tends to be greatest in the summer months. In the winter much of the precipitation above 3,000ft falls as snow. There are no climate stations or even isolated rain gauges in the survey area. The nearest climate records are from Milford Sound to the north, Te Anau to the east, and Doubtful Sound and Wilmott Pass to the south. Milford Sound and Doubtful Sound have long-term average annual rainfalls of

253in. and 226in. respectively. Wilmott Pass has 281in. annually but at Te Anau the rainfall is only around 50in. (N.Z. Met. Service, 1969). It can be assumed that the rainfall of the survey area is more than 200in. west of the Main Divide but drops towards the south-east, until, in the extreme east of the Murchison Range it is probably less than 80in.

The botany and ecology of the forests and scrublands of the area have never been satisfactorily described. The most thorough account to date is published in the report of the New Zealand-American Fiordland Expedition (Poole, *et al.* 1951). This account describes the important forest and scrub types between George Sound, Caswell Sound, and the Middle Fiord of Lake Te Anau and highlights some of the more interesting features of the vegetation-habitat relationships of the area such as the unusual plant succession on the steep glaciated valley sides. Forest succession on landslides above Lake Thomson, at the head of the north-west arm of the Middle Fiord of Lake Te Anau has been further described by Mark *et al.* 1964. Scott *et al.* 1964 have described altitudinal variation in forest composition near Lake Hankinson, but the vegetation outside this George Sound-Caswell Sound-Middle Fiord area has never been fully studied, and only broad accounts of it exist (Holloway 1954, Cockayne 1928).

The following account of the animal history of the survey area is from K. Tustin (pers. comm.). The first herbivorous mammal to be introduced into the area was the opossum (*Trichosurus vulpecula*) in the early 1890s. Subsequent liberations up to 1930 have resulted in a local opossum population at Milford Sound, and light but more widespread populations around the western shores of Lake Te Anau. Wapiti (*Cervus canadensis*) were liberated in George Sound in 1905, and red deer (*Cervus elaphus*) infiltrated into the area, mostly from the south, and became widespread by the 1950s. Most of the survey area could be considered to have experienced peak populations during the 1940s to early 1960s, with the central survey areas first affected. The north-western area is an exception and is still in the stages of colonisation.

Scattered reports of chamois (*Rupicapra rupicapra*) throughout the area have been reported and some hare (*Lepis europaeus*) signs seen but these animals are, as yet, of little significance in the animal-plant interrelationships.

TECHNIQUE

Field Measurements

Sociological descriptions of 1,053 stands throughout the area, form the basis of the present report. A further 25 permanent plots will form datum points to aid interpretation of future changes which may occur in the vegetation. The layout and measurement of these permanent plots will be described elsewhere. Nine hundred and thirteen of the sociological descriptions or temporary plots were located at 147.6ft (135m) intervals along 84 alitudinal transects. The starting points of these transects were chosen in a restricted random fashion along the major stream beds. In each case the direction of the transect followed the compass bearing representing the shortest distance plus 5° from the random starting point to the top of the scrub belt (Fig. 1). The remaining 140 temporary plots were located in off-line positions. These were subjectively placed in representative stands of minor forest and scrub associations not sampled, or sampled only rarely by the on-line plots in an area.

Five tiers of vegetation were delineated by these heights: stand top height, 40ft, 15ft, 6ft, 1ft, and ground level. All species of vascular plants in each tier were listed; epiphytes and parasites were recorded separately. An estimate was made of the physiognomically dominant species and of the density of vegetation in each tier. The aspect, altitude, slope, physiography, parent rock, soil drainage, and mean soil depth (measured with metal probes) at the site of each temporary plot were recorded. The percentages of soil surface covered by moss, litter, living vascular plant material, bare soil and rock were estimated. Rock material visible on the soil surface was recorded as being loose rock or parent rock and an estimate made of whether loose rock particles were predominantly greater than or less than 1ft in diameter. Species of vascular plants which showed obvious ungulate browse were noted and the degree of browse recorded as light, moderate, or heavy.

Analysis

(a) *Associations*

The 1,053 temporary plots were divided into 16 associations using the numerical procedure described below. Two hundred plots were randomly selected from the total and an index of similarity, "Sorensen's k" was calculated between each pair of plots. This involved assigning each species in each plot an "importance rating" based on physiognomic dominance. Physiognomic dominant species were rated 100 points, other species 50 points, and comparisons were made on the basis on importance ratings shared, over total importance ratings. The highest indices of similarity were progressively clustered using a multilinkage technique (Wardle, 1970) until 16 groups of more than three plots each remained. The mean importance rating for each species in each of these groups was calculated and all 1,053 plots were then tested against the 16 groups, again using "Sorensen's k"*. Each plot was subsequently placed into the group with which it had the highest similarity. The mean importance rating for each species in each of these enlarged groups was then calculated and the placing of the individual plots again tested. The final groupings of the 1,053 plots became the associations.

The mean structure and habitat and the composition of each of the 16 associations were calculated. The survey area was divided into seven more-or-less equal-sized units (Fig. 7) and the proportion of the forest and scrub composed by each association in each unit calculated from the random on-line plot frequencies.

(b) *Animal-plant inter-relationships*

The susceptibility of the vegetation and the current and past use of it by red deer and wapiti has been calculated. The methods are explained below.

Susceptibility: The susceptibility of the larger ferns, shrub and tree species has been derived from tier analysis of the plots which showed evidence of red deer or

* If the IBM360 computer at Ilam, used in the analysis, had contained adequate storage, a clustering of the total 1,053 plots could have been carried out in one operation so that the procedure of testing individual plots against groups formed from the randomly chosen 200 plots would have been unnecessary.

wapiti presence in the form of browsing, tracking, or pellets. Vegetation in the 1ft to 6ft tier is nearly always available for browsing by red deer or wapiti while at least some of the vegetation in the less than 1ft and 6ft to 15ft tiers is outside the normal browse range as it is either too close to the ground or too high. The frequency of a species is thus likely to become reduced by browsing in the 1ft to 6ft tier long before it becomes affected in the less than 1ft or 6ft to 15ft tiers. Browse susceptible species are likely to suffer greater reduction within the 1ft to 6ft tier relative to outside it than those which are more tolerant. This relationship of frequency of a plant species inside the 1ft to 6ft tier relative to outside it has been used to determine the relative susceptibility or susceptibility ratings (SR) for each of the major species. The rating was calculated by the following formula for species which normally grow to between 1ft and 6ft in height:

$$SR = \frac{\text{Frequency} < \text{1ft tier}}{\text{Frequency 1ft to 6ft tier}}$$

This was refined for species that normally grow greater than 6ft high by applying the formula:

$$SR = \frac{\frac{1}{2}\ (\text{Freq.} < \text{1ft tier} + \text{Freq. 6ft to 15ft tier})}{\text{Frequency 1ft to 6ft tier}}$$

The susceptibility of the 16 associations has been determined by calculating the mean susceptibility of the species forming the overstorey. The following formula has been used:

$$\text{Susceptibility of association} = \frac{\Sigma\ (IR \times SR)}{\Sigma\ IR}$$

where IR = Importance Rating (Frequency weighted 2 : 1 towards dominance) for each overstorey species in association.

and SR = Susceptibility rating for species with importance rating IR.

Overstorey species are tree species only in forest associations and all species which normally grow over 1ft in height in sub-alpine scrub associations. The susceptibility of the understorey of forest associations has been determined similarly but instead of overstorey species, shrub and herb species which normally grow to over 1ft in height have been used in the calculation.

The susceptibility of the seven sub-areas of the survey area (Fig. 7) to browsing by ungulates depends on the relative susceptibility of the associations which compose the forest and scrub in each.

Current utilisation: Current utilisation by red deer and wapiti of the individual vascular species, the associations, and the sub-areas within the survey area have been calculated from browse records. The relative utilisation of the individual species was determined by calculating a browse index for each. This was the frequency of recorded browse on the species weighted 3 : 2 : 1 dependent on whether it was heavy, moderate, or light. This index does not take into account the actual frequency of the species and thus cannot be used to indicate order of browsing preference. However, it does indicate the relative importance of each species in providing fodder for red deer and wapiti. The approximate percentage of the total fodder provided by each species has been calculated as:

$$\frac{\text{Browse index of species}}{\Sigma \text{ Browse indices of all species}} \times \frac{100}{1}$$

Current utilisation of each association has been determined by calculating separately for the 12 species with the highest browse indices over the total survey area, a weighted browse frequency from all plots in the association. This is given by the following formula:

$$\text{Weighted \% browse frequency} = \frac{\text{BI}}{\text{F (1ft to 6ft tier)}} \times \frac{100}{1}$$

where BI = Browse index of the species calculated for an association
and F = Total frequency of the species in the 1ft to 6ft tier of the association.

The weighted % browse frequency represents the degree to which available foliage of the species has been utilised in the association. The relative current utilisation of the 16 associations is derived by ranking them in order of this index for each of the 12 species and deriving the mean ranking order.

Current utilisation of the blocks within the survey area has been determined in the same way. The weighted % browse frequency was worked out for the 12 species in each block. Ten blocks were recognised for this calculation (Fig. 7). These were numbered from 1 to 7 but 5, 6, and 7 were further subdivided into a and b units.

History of utilisation: The history of utilisation of the associations and sub-areas has been determined from the degree of modification in the 1ft to 6ft tier. Twelve species were chosen to indicate the degree of modification. These "indicator species" were required to be fairly common throughout the survey area, to occur in a large proportion of the 16 associations and 10 sub-areas, and to represent a range from highly susceptible to moderately tolerant to damage from browsing. Formulas similar to the susceptibility rating formula were used to calculate the degree of modification for each indicator species in each of the associations and sub-areas. The only difference with these formulas was that all plots were used in the calculation of frequency and not just those with animal sign. The associations and areas which gave the highest indices for the most susceptible species were regarded as the ones which had suffered the greatest degree of modification in the past and thus sustained the heaviest use by ungulates.

THE ASSOCIATIONS

The 16 associations recognised have been classified as follows:

Class 1 — Subalpine scrub
- S1 — Short *Hebe**-*Dracophyllum* scrub
- S2 — Tall *Senecio* scrub
- S3 — Silver beech-*Dracophyllum* scrub

* Botanical names used in this paper are according to Zotov (1963) for the grass sub-family **Arundinoideae,** Cheeseman (1925) for the remainder of the indigenous Monocotyledons, Philipson (1965) for the genera of the **Araliaceae,** and Allan (1961) for all remaining species.

Class 2 — Complex forests dominated by silver beech
- C1 — Silver beech-*Archeria-Senecio* forest
- C2 — Silver beech-*Coprosma* forest
- C3 — Silver beech-pepperwood-*Blechnum* forest
- C4 — Kamahi-silver beech-*Cyathea* forest

Class 3 — Complex forests with a large mountain beech component
- M1 — Silver beech-rata-kamahi-mountain beech forest
- M2 — Mountain beech-*Phyllocladus* forest
- M3 — Mountain beech-manuka-*Dacrydium* forest

Class 4 — Mixed scrub-hardwood forest
- P1 — Lacebark-*Polystichum* forest
- P2 — Silver beech-lacebark-*Polystichum* forest
- P3 — Mahoe-pate-*Cyathea* forest

Class 5 — Simple mountain beech-silver beech forests
- E1 — Mountain beech-silver beech-kamahi forest
- E2 — Simple silver beech forest
- E3 — Simple mountain beech forest

The composition, structure, and habitat of each is described with species arranged in order of decreasing frequency. The percent frequency of species occurring in 50% or more of the plots in any one association is given in Table 1 and tier densities and ground cover percentages in Table 2.

S1 — Short *Hebe-Dracophyllum* scrub

This short sub-alpine scrub mostly occurs on the eastern side of the survey area. It is a minor association and forms less than 1% of the total forest and scrub. It is dominated by *Hebe odora* and *Dracophyllum uniflorum.* These, and less frequently *Coprosma ciliata* and *C. pseudocuneata,* form a dense canopy with a mean height of 5.6ft (Fig. 11). Any interscrub spaces are filled with a dense herbaceous ground cover of *Blechnum penna-marina, Polystichum vestitum, Ourisia macrophylla, Senecio lyallii, Celmisia walkeri* and *C. petiolata.*

S2 — Tall *Senecio* scrub

The tall *Senecio* scrub is again a minor association and though it occurs throughout the survey area it forms only 1% of the total forest and scrub. It has an affinity for steep gully sites above timberline. It is taller than S1 and the canopy, which is dominated by *Senecio bennettii, Pseudopanax colensoi* and *Dracophyllum longifolium* (Fig. 3) has a mean height of 12ft. There is a dense short scrub understorey (Table 2) mainly composed of species important in S1 (Table 1). The major species in this tier are *Coprosma pseudocuneata, C. serrulata, Dracophyllum uniflorum, Phormium colensoi, Hebe odora, Coprosma astonii* and *Gaultheria crassa. Olearia crosby-smithiana,* a woody species restricted to Fiordland, can sometimes be important in this association. There is a dense ground cover of *Anisotome haastii, Chionochloa flavescens, Ourisia macrophylla* and *Polystichum vestitum* but the Celmisia species, important in association S1, occur only occasionally.

TABLE 1—The percent frequency of species occurring in 50% or more of the plots in any one association

Species	ASSOCIATION															
	Class 1			Class 2				Class 3			Class 4			Class 5		
	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Anistome haastii	42	76	64	5							16	1				5
Archeria traversii		32	41	83	51	3	4	67	82			16		2	13	35
Aristotelia serrata					6	33	7				24	20	68	2		2
Asplenium bulbiferum					2	15	37					8	85	7		
Asplenium flaccidum				42	87	84	84	63	23	4	32	81	51	50	27	
Astelia cockaynei	7	36	32	82	82	18	60	88	71	9	8	49	48	2		23
Blechnum capense		24	6	19	54	79	57	69	30	9		20	40	44		2
Blechnum discolor				1	63	88	89	68	15			4	28	76		
Blechnum fluviatile		4		6	50	52	32	10			28	57	40	5		
Blechnum minus		4	16	26	62	49	39	39	61	31	4	15	22	44		2
Blechnum penna-marina	92	32	16	13		7			2		32	16		2		8
Cardamine debilis	7	8				1					88	25	8			
Carpodetus serratus				1	34	83	56	13	7			18	65	47		
Celmisia petiolata	50	24	22	1					2							
Celmisia walkeri	50	32	45	6					2		4	1				14
Chionochloa acicularis	7	28	54	27	1				10	13						8
Chionochloa flavescens	21	60	74	11					5							
Coprosma astonii	14	68	16	72	88	50	12	51	2		64	90	11	7	18	11
Coprosma ciliata	64	36	3	31	45	26	33	8	5		92	83	5	13	13	20
Coprsoma colensoi			3	10	73	26	69	88	64	36		18	8	13		
Coprosma foetidissima		4	9	52	100	92	97	100	84	45	8	60	45	89	4	
Coprosma lucida					6	30	40	21	20			1	62	39		
Coprosma pseudocuneata	64	92	87	98	43	3	5	55	66	22	8	44		10	22	100

TABLE 1— Continued

Species	ASSOCIATION															
	Class 1			Class 2				Class 3			Class 4			Class 5		
	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Coprosma serrulata	21	84	64	9			1				4			2		
Cyathea smithii				1	31	50	87	17	2	4		17	88	13		
Cyathodes juniperina			3					14	38	90				2		2
Dacrydium biforme			29	5				9	53	68						17
Dacrydium intermedium								3	28	59						
Dracophyllum longifolium	7	76	48	47	4			18	58	100			2	2		29
Dracophyllum menziesii		36	74	9				3	15	18					4	
Dracophyllum uniflorum	85	84	93	13					2	13						44
Elaeocarpus hookerianus					6	16	30	46	51	22				28		
Erechtites sp.	28					1					64	9				
Forstera sedifolia	14	16	51	4					2	4						8
Fuchsia excorticata		4			16	41	15				28	36	77	2		
Gaultheria crassa	14	56	19	4					2						4	5
Gaultheria depressa	35	36	77	41					15	9		1			13	70
Grammitis billardieri		20	9	38	78	83	68	82	43	31		57	8	94	31	23
Griselinia littoralis	7			18	99	98	97	95	66	27	32	79	74	65		
Hebe odora	100	76	29	8					2	18	4	2				2
Hedycarya arborea							41	1					65			
Hoheria glabrata	14	16		3	13	20	10				100	84	34			
Hymenophyllum multifidum	28	36	70	88	42	37	12	60	76	22	8	60	2	63	77	79
Hypolepis millefolium	7			4	5	11					68	21	2	2		
Leptospermum scoparium						1		2	10	95			2	2		
Lycopodium fastigiatum	42	12	58	8	1				2	4						2
Melicytus ramiflorus						5	29		2				82			
Metrosideros diffusa					5	11	71						57	7		
Metrosideros umbellata				6	64	37	63	90	66	77		4	34	55		2
Myrsine australis					1	13	56	5	2			1	40	7		

TABLE 1— Continued

Species	ASSOCIATION															
	Class 1			Class 2				Class 3			Class 4			Class 5		
	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Myrsine divaricata	7	20	12	81	85	71	56	86	89	22	28	85	20	28	4	38
Nertera dichondraefolia				1	51	79	77	31	2		20	57	37	36		
Nothofagus solandri v. cliff.		4	6	19	10	22	10	62	97	95		12		94	59	91
Nothofagus menziesii	7	36	87	100	98	98	91	95	76	22	52	96	42	89	100	61
Olearia colensoi		36	61	26	7			14	17	22		3	2			2
Olearia ilicifolia	7	4	3	4	2						60	20	5			
Ourisia macrophylla	64	52	45	16	15			9	2		8	20	2			
Phormium colensoi	28	80	70	38	10	1		14	10	22		3	2	2		2
Phyllocladus alpinus	21	12	25	13	3	18		37	92	63		2		47	9	79
Phymatodes diversifolium					7	26	72	12	2		4	11	82	2		
Pittosporum crassicaule		16	35	52	34	1	2	55	58	18	8	19				38
Podocarpus ferrugineus					3	13	56	18	12				14	63		
Podocarpus hallii					5	33	32	64	53	18			2	60	4	5
Polystichum vestitum	85	52	3	34	45	60	20	3			100	94	62	15	18	5
Pseudopanax colensoi	7	80	61	78	76	43	67	82	51	68	12	53	45	55	13	17
Pseudopanax crassifolum		4		1	20	67	77	34	17			8	28	97		2
Pseudopanax lineare		16	12	46	67	5	7	81	84	54		16				11
Pseudopanax simplex		16		53	98	77	81	98	94	31	4	78	5	81	9	8
Pseudowintera colorata		4		7	86	88	83	52	5		24	68	37	26		
Ranunculus hirtus	21		3	8	7	9		1			100	50	17	2		2
Rubus cissoides				1	35	58	26	6	2		4	35	31	42		
Schefflera digitata					7	33	63					15	85	2		
Schizaea fistulosa									2	50						
Senecio bennettii	14	92	41	71	52	1	5	35	25	13	4	27	8		4	2
Senecio lyallii	64	24	29	5	1			1			12	2		2		2
Uncinia filiformis	14	24	3	66	82	16	33	64	30		48	67	8		36	44
Urtica incisa						1					52	3	2			
Weinmannia racemosa					61	81	100	86	53	54		5	77	86		

TABLE 2—Stand densities. The mean density of each tier in each association is given. This is developed by use of ground cover percentages for the < 1ft tier and by a tier density index for the remaining four tiers. The index is calculated by the following formula:

$$\frac{3\ (\text{f dense}) + 2\ (\text{f med.}) + 1\ (\text{f open})}{3\ (\text{total No. of plots})} \times \frac{100}{1}$$

where f = frequency of plots with dense, medium or open tiers.

TIER		ASSOCIATION															
		Class 1			Class 2				Class 3			Class 4			Class 5		
		S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Tier Density Index	T_1 (40ft+)	0	0	0	18	47	57	57	42	13	0	8	47	15	63	56	21
	T_2 (15ft-40ft)	0	3	10	47	65	77	72	69	63	21	53	62	77	67	55	55
	T_3 (6ft-15ft)	2	29	33	78	75	69	64	74	79	71	47	63	73	64	73	63
	T_4 (1ft- 6ft)	81	94	85	72	69	63	78	69	84	86	84	69	78	68	68	61
Percent Ground Cover T_5 (< 1ft)	M	10.0	12.0	12.6	35.1	34.7	32.9	28.4	43.3	51.2	35.9	33.2	41.8	14.4	38.8	41.4	35.5
	L	21.3	33.6	24.2	25.9	37.8	43.4	39.5	32.3	24.5	22.7	15.6	24.7	40.0	37.1	35.9	40.0
	V	61.4	43.2	51.9	32.8	20.3	14.9	23.4	20.4	21.4	26.8	35.0	22.6	24.5	20.3	20.5	18.9
	B	2.0	5.6	3.5	4.3	5.7	6.7	6.7	2.0	2.9	3.2	3.4	7.6	16.1	3.6	2.2	4.7
	R	5.3	5.6	7.8	1.9	1.5	2.1	2.0	2.0	0	11.4	12.8	3.3	5.0	0.2	0	0.9

M = Moss L = Litter V = Vascular vegetation < 1ft high B = Bare soil R = Rock

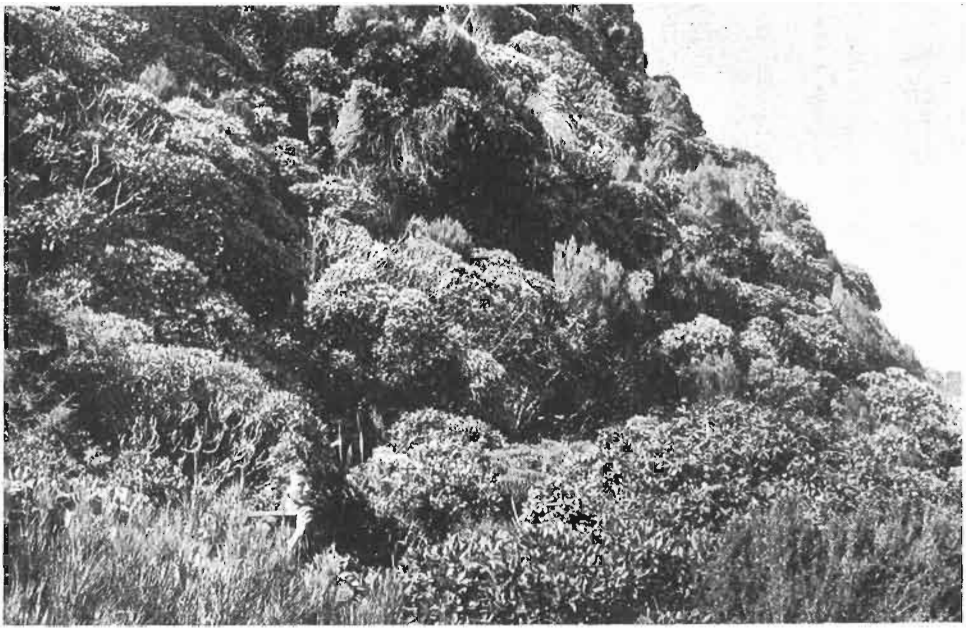

FIG. 3—Tall **Senecio** scrub above timber line in the Transit catchment. This scrub is dominated by **Senecio bennettii, Pseudopanax colensoi,** and **Dracophyllum longifolium.**

S3 — Silver beech-*Dracophyllum* scrub

This association is transitional between forest and sub-alpine scrub. It occupies steep valley sites and covers 2%-5% of the total forest and scrub area. It is composed of well-spaced silver beech (*Nothofagus menziesii*) trees forming an open canopy about 14ft high. In the canopy gaps there is a dense scrub of *Dracophyllum uniflorum, Coprosma pseudocuneata, Dracophyllum menziesii, Phormium colensoi, Coprosma serrulata, Pseudopanax colensoi* and leatherwood (*Olearia colensoi*). The ground is densely vegetated (Table 2) with *Gaultheria depressa, Hymnophyllum multifidum, Anistome haastii, Lycopodium fastigiatum* and *Forstera sedifolia. Chionochloa flavescens* and *C. acicularis* are important in clearings.

C1 — Silver beech-*Archeria-Senecio* forest

Silver beech-*Archeria-Senecio* forest—is a major association in the Worsley-Glaisnock area in the north-east and the Charles Sound area in the south-west. It is also important elsewhere on the western side of the survey area and altogether forms about 18% of the total forest and scrub. It is restricted to high altitude sites, mostly on the north and west facing slopes and spurs and is one of the main associations forming the timberline. Silver beech entirely dominates the canopy which is fairly open and has a mean top height of 37ft. There is usually a sub-canopy of *Senecio bennettii* and less frequently *Pseudopanax simplex.* The shrub tiers are generally dense and are dominated by *Coprosma pseudocuneata, Archeria traversii, Myrsine divaricata,* *Pseudopanax colensoi* and *Coprosma astonii. C. foetidissima* and *Pittosporum crassicaule* may also be present. There is an open low herb tier of scattered *Astelia cockaynei* and *Uncinia filiformis* but the ground cover of *Hymenophyllum multifidum* and moss is usually fairly complete.

C2 — Silver beech-*Coprosma* forest

This is again a major association and forms about 20% of the total forest and scrub area. It is particularly important in the mid-west and south-west but becomes less important to the east until, in the eastern Murchison Range, it is absent. It occupies the upper mid slopes, below association C1. Again it is mostly restricted to north and west slopes and has an affinity for spur sites. The canopy is denser and taller than in association C1 with a mean top height of 54ft. Silver beech is again the dominant tall tree species, but in this association it may be associated with rata (*Metrosideros umbellata)* and kamahi (*Weinmannia racemosa*). There is a dense sub-canopy of broadleaf (*Griselinia littoralis*), *Pseudopanax simplex* and *P. colensoi* and sometimes *P. lineare* and *Senecio bennettii.* The shrub tiers are usually dense and are dominated by the *Coprosma* species; *C. foetidissima, C. astonii* and *C. colensoi. Pseudowintera colorata, Myrsine divaricata* and sometimes *Archeria traversii* may also be important species. There is a fairly complete ground cover of *Astelia cockaynei, Grammitis billardieri, Blechnum discolor,* and *B. minus* and less often *B. capense, Nertera dichondraefolia* and *Blechnum fluviatile.*

C3 — Silver beech-pepperwood-*Blechnum* forest

This association occupies lower mid slopes and terraces below association C2. It is moderately important throughout, forming about 5% of the total forest and scrub. The canopy is fairly dense and is again dominated by silver beech and often kamahi. Rata, an important species in association C2, occurs only occasionally (Table 1). This is one of the tallest associations in the area (Fig. 11) and has a mean top height of 61.4ft. The sub-canopy is dense (Table 2) and is dominated by broadleaf, putaputaweta (*Carpodetus serratus*), *Pseudopanax simplex,* and lancewood (*P. crassifolium).* The shrub tiers are relatively open compared with the other associations and the main species are *Coprosma foetidissima* and pepperwood (*Pseudowintera colorata*), and less often, *Myrsine divaricata, Coprosma astonii* and *Cyathea smithii.* There is a well developed tall herb layer of *Blechnum discolor, B. capense* and sometimes *Polystichum vestitum* but ground cover is sparse with litter, bare soil and a scattering of *Grammitis billardieri, Nertera dichondraefolia* and *Blechnum fluviatile. Asplenium flaccidum* is an important epiphyte and the liane *Rubus cissoides* is often present.

C4 — Kamahi-silver beech-*Cyathea* forest

This association which forms 12% of the total forest and scrub is restricted to low altitudes on the western side of the survey area. It is most important in the north-west, gradually becoming less important to the south-west. It usually occurs on northern facing slopes and terraces, and is the most complex association in the survey area with a mean number of vascular species per plot of 31.6 (Fig. 12). The canopy is fairly dense, has a mean top height of 59ft and is dominated by kamahi. Silver beech is usually present, and there may be some rata, miro (*Podocarpus ferrugineus*) and occasional rimu (*Dacrydium cupressinum*). There is a fairly dense sub-canopy of broadleaf, the tree fern *Cyathea smithii, Pseudopanax simplex,* lancewood, *P. colensoi, Schefflera digitata, Myrsine australis* and putaputaweta. The shrub tiers are fairly open with *Coprosma foetidissima* and pepperwood as the dominant species and there may be some *C. colensoi* and *Myrsine divaricata.* The ground cover, which is also fairly open, is formed by *Blechnum discolor, Nertera dichondraefolia* and *Metrosideros diffusa,* and to a lesser extent by *Grammitis billardieri, Astelia cockaynei* and *Blechnum capense.* The fern species *Asplenium flaccidum* and *Phymatodes diversifolium* often occur as epiphytes.

M1 — Silver beech-rata-kamahi-mountain beech forest

Association M1 forms about 13% of the total forest and scrub. It is important on the western side of the survey area and also along the central ranges but it is rare in the east (Fig. 7). It occurs over a wide altitudinal range on the mid-slopes and has an affinity for spur sites. The canopy which has a mean top height of 50.8ft is co-dominated by silver beech, rata, kamahi, Hall's totara and mountain beech (*Nothofagus solandri* var *cliffortioides*) (Fig. 4) and there is a fairly dense sub-canopy of *Pseudopanax simplex,* broadleaf, *P. colensoi* and *P. lineare.* The shrub tiers are moderately dense and are dominated by *Coprosma foetidissima, C. colensoi, Myrsine divaricata* and *Archeria traversii,* and *Coprosma pseudocuneata, Pittosporum crassicaule, Pseudowintera colorata* and *Coprosma astonii* may also be important. There is a fairly open herbaceous tier of

FIG. 4—Silver beech-rata-kamahi-mountain beech forest in the Transit catchment. This area has only had light use by ungulates and consequently the understorey is dense and has many highly susceptible species in it.

Astelia cockaynei, Grammitis billardieri, Blechnum capense, B. discolor and *Uncinia filiformis* but the ground cover of *Hymenophyllum multifidum* and moss is fairly complete. *Asplenium flaccidum* often occurs as an epiphyte.

M2 — Mountain beech-*Phyllocladus* forest

Mountain beech-*Phyllocladus* forest is a minor association forming only 3% to 4% of the total forest and scrub. It is mainly restricted to low fertility soils developed on slow weathering parent rock and to poorly drained areas. It mostly occurs in the region between Milford Sound and Poison Bay, and near the heads of Middle and South Fiords of Lake Te Anau. Mountain beech, which is the dominant tree species, is more important than in association M1 (Table 1). It forms a canopy with a mean top height of 38ft as compared with 50.8ft for M1 (Fig. 11). Other tree species often associated with mountain beech include silver beech, rata, Hall's totara, kamahi, and pokaka (*Elaeocarpus hookerianus*). There is a moderately dense sub-canopy of *Pseudopanax simplex, P. lineare* and broadleaf, and a dense shrub tier of *Phyllocladus alpinus, Myrsine divaricata, Coprosma foetidissima, Archeria traversii* and often *Coprosma pseudocuneata, C. colensoi, Dracophyllum longifolium, Pittosporum crassicaule* and pink pine (*Dacrydium biforme*). The ground has a fairly complete cover of moss, *Hymenophyllum multifidum, Blechnum minus,* and scattered *Astelia cockaynei.*

M3 — Mountain beech-manuka-*Dacrydium* forest

This association is again a minor one, forming only about 2% of the total forest and scrub. The distribution is similar to M2. Again it is mainly restricted to the Milford-Poison Bay area and to the region near the heads of the middle and south

FIG. 5—Mountain beech-manuka-**Dacrydium** forest in the Transit catchment.

fiords of Lake Te Anau. It occurs over a wide altitudinal range on the mid slopes and is usually associated with shallow, low fertility soils developed on slow-weathering parent rock. The mean soil depth for the plots in the association was only 7.7in. Sometimes it grows on poorly drained sites. The canopy is open with a mean top height of only 19.5ft and dominants range from mountain beech, manuka (*Leptospermum scoparium*) and yellow-silver pine (*Dacrydium intermedium*), to mountain beech and pink pine. Other canopy species include *Dracophyllum longifolium,* rata, and less commonly, *Pseudopanax colensoi* and *Phyllocladus alpinus.* Sometimes this association occurs as a low scrub (Fig. 5). The scrub understorey is dense but simple, the main species being *Cyathodes juniperina* and regeneration of pink pine and manuka. There are few herbaceous species and the ground cover usually consists of branches, and regeneration of the above species. A small fern species, *Schizaea fistulosa,* is frequently present in this association, but seldom occurs outside it.

P1 — Lacebark-*Polystichum* forest

Lacebark-*Polystichum* forest forms only about 1% of the total forest and scrub. It is locally important though, especially in the east and south, forming a seral forest mainly on river terraces and rock debris fans. The soil under the stands is shallow, with a mean depth of only 5.3in., developed over broken rock fragments. Given stability this association rapidly develops into association P2 described below, and then into C1, C2, and C3. The canopy is formed almost entirely by lacebark (*Hoheria glabrata*) (Fig. 6) though occasionally there may be scattered emergent trees of silver

FIG. 6—Lacebark-**Polystichum** forest in the Worsley catchment. This association forms a seral cover on terraces and debris fans. It is very susceptible to damage from ungulates. This photograph shows an understorey which is modified by animal use.

beech. The canopy is moderately open and has a mean height of only 31ft (Fig 11). The shrub tier is also open and the main species are *Coprosma ciliata, C. astonii* and *Olearia ilicifolia.* There is usually a dense 1ft to 3ft high ground cover of *Polystichum vestitum,* but where this fern is absent the herbs *Ranunculus hirtus, Cardamine debilis, Erechtites* sp., and *Urtica incisa* give only partial cover.

P2 — Silver beech-lacebark-*Polystichum* forest

This major association forms about 9% of the total forest and scrub. It occurs throughout but is particularly important in the Worsley-Glaisnock-Lugar Burn area. It forms a seral vegetation on rock debris slopes and on terraces in the middle to upper forest belt. The soil is better developed than under association P1 stands and the mean depth is 11.2in. It replaces association P1 in the succession and eventually gives way to associations C1, C2, and C3. It is taller and more complex than association P1 (Figs. 11 and 12) but has a similar composition. Lacebark remains the main species in the sub-canopy but it is frequently associated with broadleaf, *Pseudopanax simplex* and less often *P. colensoi.* Silver beech is almost always present as an emergent dominant forming an open canopy with a mean top height of 53ft. The shrub tier is again dominated by *Coprosma astonii* and *C. ciliata* but in this association it is enriched by the addition of *Myrsine divaricata,* pepperwood, and *Coprosma foetidissima* and is usually fairly dense. As in P1, *Polystichum vestitum* forms a fairly dense ground cover but other herb species have increased. The most important of these are *Uncinia filiformis, Blechnum fluviatile, Grammitis billardieri, Nertera dichondraefolia* and *Ranunculus hirtus. Asplenium flaccidum* often occurs as an epiphyte.

P3 — Mahoe-pate-*Cyathea* forest

Association P3 is restricted to low altitude rock debris slopes and terraces on the western side of the survey area. It forms only 2% to 3% of the total forest and scrub and it mostly occurs in the Milford to Bligh Sounds area where it is seral and develops into association C4 if the site remains stable. The canopy, which is dense and has a mean top height of 40ft, is dominated by pate (*Schefflera digitata*), mahoe (*Melicytus ramiflorus*), fuchsia (*Fuchsia excorticata*), kamahi, broadleaf, wineberry (*Aristotelia serrata*) and putaputaweta. The understorey is dense and composed of saplings of the above species plus *Cyathea smithii,* pigeonwood (*Hedycarya arborea*) and *Coprosma lucida.* There is an open ground cover of *Asplenium bulbiferum, Phymatodes diversifolium* and sometimes *Polystichum vestitum* and *Metrosideros diffusa. Asplenium flaccidum* is often present as an epiphyte.

E1 — Mountain beech-silver beech-kamahi forest

This association, which forms about 4% of the total forest and scrub, occupies the lower slopes on the eastern side of the survey area, particularly in the Murchison and Stuart Mountains. The soil is well developed under the stands and the mean depth to rock is 17.4in. Mountain beech, silver beech and kamahi co-dominate and these species, and sometimes miro, Hall's totara and rata form a dense canopy with a mean top height of 65ft. This is the tallest association in the survey area (Fig. 11). There is a dense sub-canopy of lancewood, *Pseudopanax simplex,* broadleaf, and often *P. colensoi,* and an open shrub tier in which the only important species is *Coprosma foetidissima.* The ground cover is sparse and the main species are *Blechnum discolor, Grammitis billardieri* and *Hymenophyllum multifidum.* Occasionally *Asplenium flaccidum* occurs as an epiphyte.

E2 — Simple silver beech forest

This association is almost entirely confined to the middle and upper forest belt in the eastern Stuart and Murchison Ranges. It forms only 2% of the total forest and scrub. Soil is better developed under this association than under the others and the mean soil depth is 19.4in. It is the least complex association in the survey area and has a mean of only six vascular species per plot (Fig. 12). The canopy has a mean top height of 52ft and is dominated by silver beech but sometimes mountain beech is also present. The sub-canopy and shrub tiers are almost entirely composed of regeneration of these tree species. The forest floor has a fairly complete cover of *Hymenophyllum multifidum* and moss but other herbaceous species are usually not present.

E3 — Simple mountain beech forest

Association E3 is almost entirely confined to high altitudes in the eastern Murchison Range where it is the main timber-line forest. It forms only about 4% of the total forest and scrub in the survey area. It has a low complexity with a mean of only 12 species of vascular plants per plot. The canopy, which has a mean top height of 38ft, is dominated by mountain beech which is sometimes associated with silver beech. There is a moderately dense shrub tier of *Coprosma pseudocuneata* and *Phyllocladus alpinus* and an open ground cover of *Hymenophyllum multifidum, Gaultheria depressa,* and moss.

The pattern of distribution of the associations is mainly related to changes in altitude and rainfall. In the drier south-easterly section of the survey area the major forest associations are E1, E2, and E3 (Figs. 7 and 10). Association E3 occupies the highest altitude sites and E1 the lower slopes (Fig 8). Association E2 may occur between them. In the wetter northern and western areas, the main forest associations are C1, C2, C3 and C4. Association C1 occurs at the highest altitudes, C2 occupies the upper mid-slopes, C3 the lower mid-slopes and terraces and C4 the lower slopes.

The main timber-line associations are C1 and E3. The timber line varies between 2,800 and 3,900 ft a.s.l. In general the eastern, and especially the south-eastern timber lines are higher than those in the west. In the east, the mean altitude is 3,550ft. In the centre the mean is 3,150ft and in the west, close to the coast, it is only 3,050ft. Thus the timber line descends rapidly westwards towards the main divide, followed by a more gradual depression towards the coast. Silver beech is the physiognomic timber-line tree. It is usually the only timber-line tree in the northern, western and central areas. In the south-east it may be joined by mountain beech, and in the extreme south-east mountain beech alone may dominate.

Above the timber line there is usually a very narrow sub-alpine scrub belt but sometimes the forest may give way directly to a *Chionochloa* tussock grassland, with scrub restricted to areas of locally lowered timber lines such as gullies and lower valley slopes. The main scrub association at higher altitudes is S1. Associations S2 and S3 tend to be transitional to forest.

Soil development and fertility are important in the distribution of the class P and

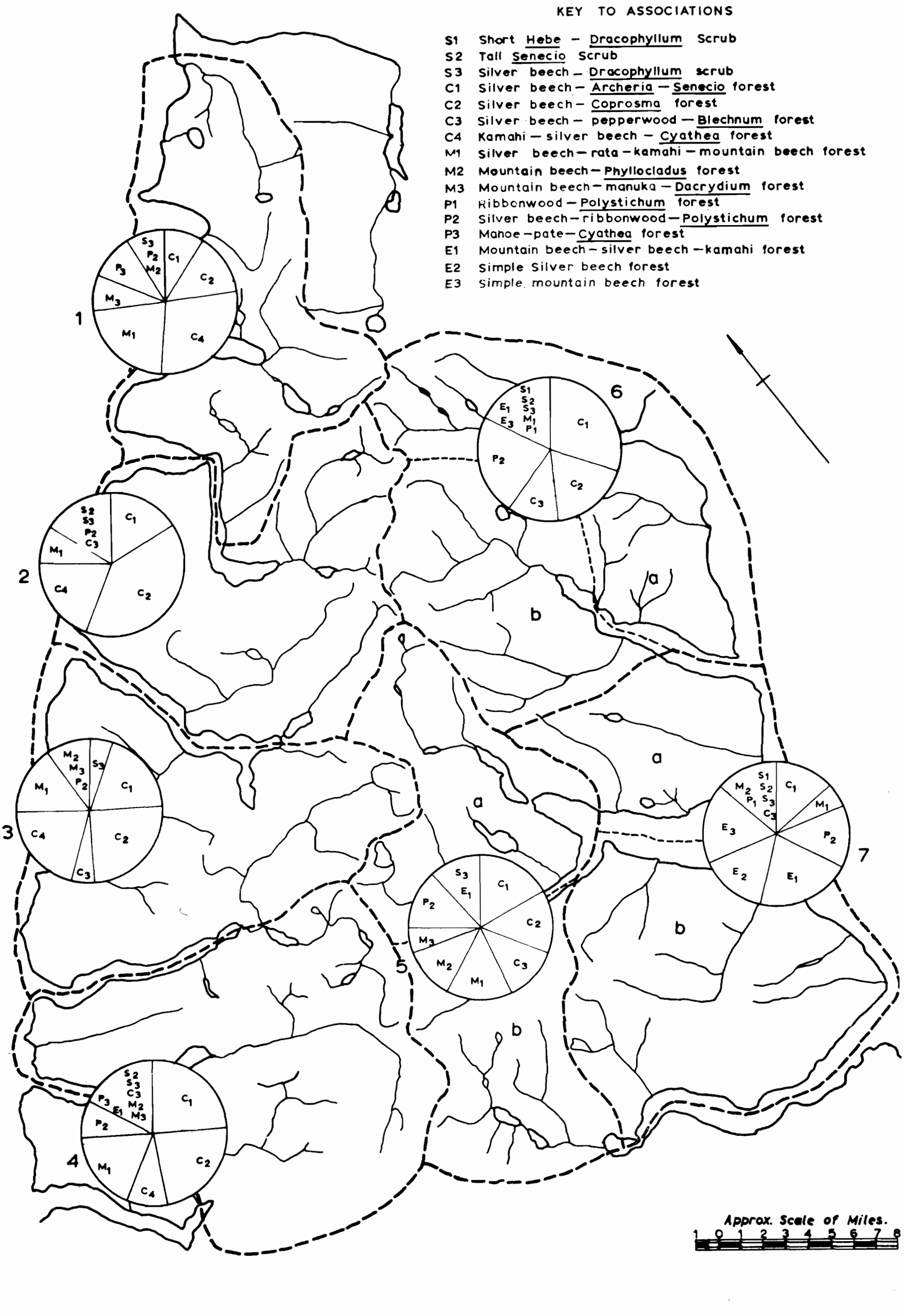

FIG. 7—Distribution of forest and scrubland associations, northern Fiordland.

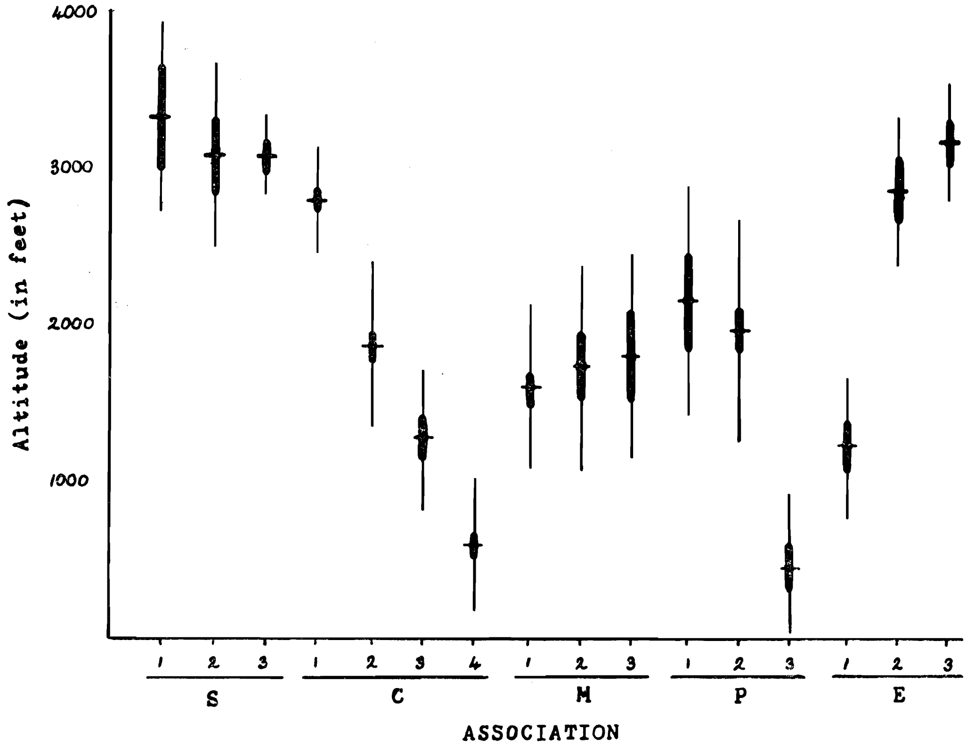

FIG. 8—Altitude. The mean, standard error (P = 0.05) and standard deviation for the plots in each association is shown.

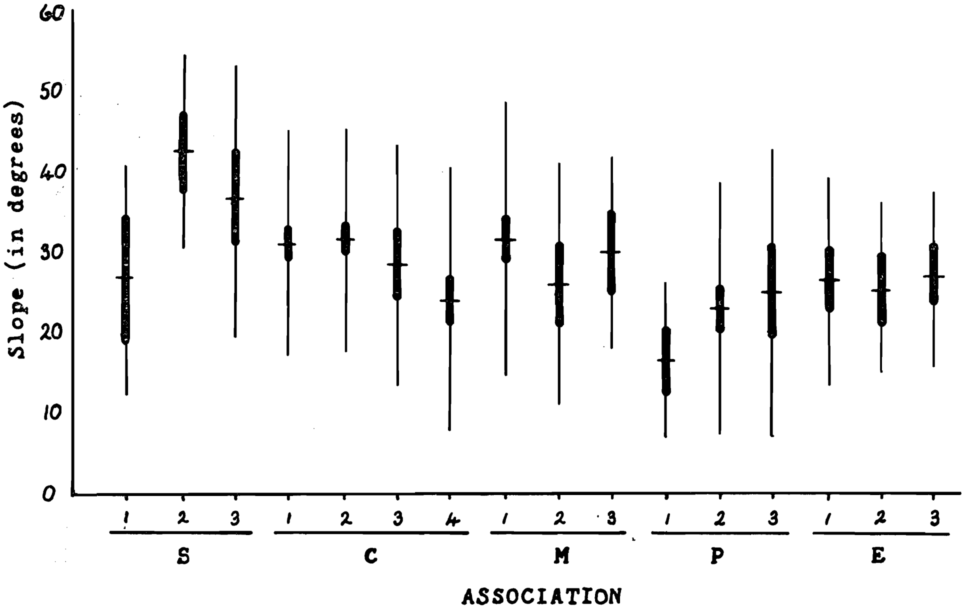

FIG. 9—Slope. The mean, standard error (P = 0.05) and standard deviation for the plots in each association is shown.

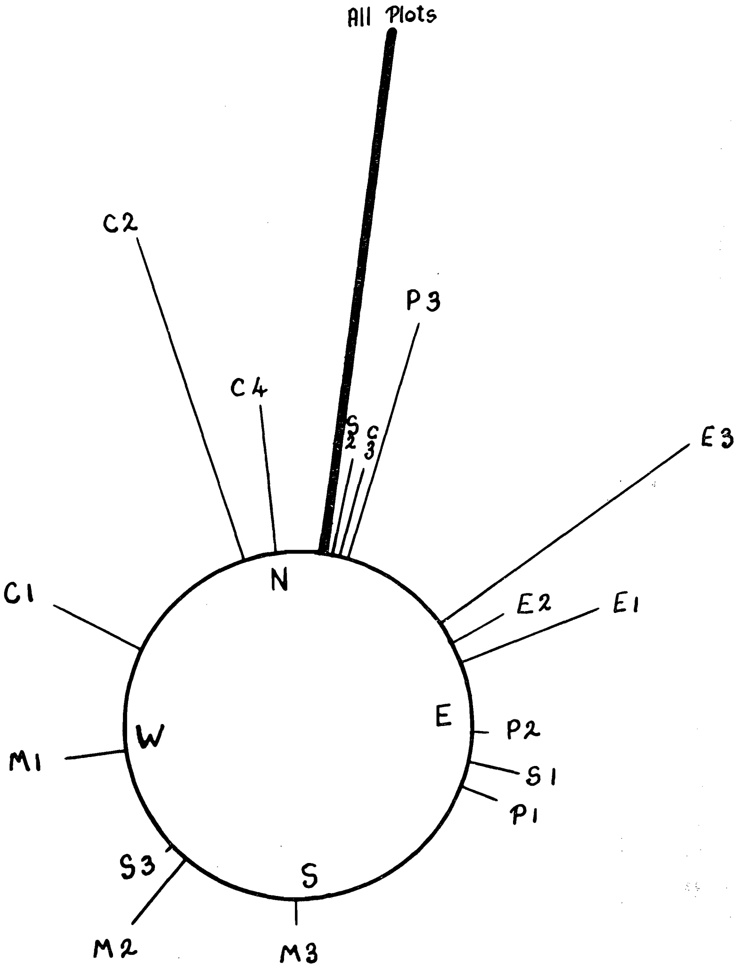

FIG. 10—Mean aspect, calculated from components, for each association. The length of the line illustrating the mean aspect represents the strength of the components in that direction and is calculated from

$$\frac{\sqrt{(\mathrm{Sin}\ \theta)^2 + (\cos\ \theta)^2}}{\text{number of plots}}$$

where θ is the aspect in degrees.

M associations. The class P associations are seral on areas of broken and river-worn rock and are usually associated with thin soils (Table 3). P1 tends to occur at the higher altitudes while P3 is restricted to low altitudes in the west (Figs. 7 and 8). Association P2 is transitional between the P1 succession and the sub-climax C associations.

Stands in the class M associations mostly occur on areas of low fertility where there is a slow-weathering parent rock, and, especially with association M2, where there are areas of poor drainage (Table 3). The poorest sites are usually occupied by M3 stands.

TABLE 3—Soil depth, drainage, soil surface features, and physiography for each association. The drainage factor has been calculated by the following formula:

$$\frac{3\ (\text{f good}) + 2\ (\text{f mod.}) + 1\ (\text{f poor})}{3\ (\text{total No. of plots})} \times \frac{100}{1}$$

where f = frequency of plots with good, moderate or poor drainage

	ASSOCIATION															
Site & Soil Factors	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Mean soil depth (inches)	7.1	7.2	8.4	10.9	11.2	11.3	11.0	10.7	13.0	7.7	5.3	11.2	8.6	17.4	19.4	13.3
Drainage factor	91	96	94	92	94	94	90	92	78	88	97	95	96	98	95	92
% plots with:																
Parent rock exposed	33	52	39	21	21	21	11	17	21	36	0	10	17	18	9	23
Loose rock exposed:																
mainly > 12in.	47	28	10	10	12	28	8	7	3	5	44	15	43	10	0	3
mainly < 12in.	20	20	19	23	20	26	31	10	3	36	40	45	14	18	5	21
No rock exposed	13	12	23	45	55	30	48	66	77	27	16	33	34	58	86	56
% Plots on:																
Face sites	53	72	77	56	64	68	61	61	61	77	60	53	51	75	73	76
Spur sites	7	16	23	40	26	7	9	30	26	18	8	10	0	11	18	24
Gully sites	27	12	0	4	4	6	7	4	3	0	8	8	20	3	0	0
Terrace sites	13	0	0	0	6	19	23	5	10	5	24	29	29	11	9	0

The tallest associations in the survey area are E1 and C3 with mean heights of 65ft and 61.4ft respectively. The stand top height decreases with increase in altitude and the shortest class E and C associations, E3 and C1, occupy the highest belts. These have mean top heights of 38ft and 37ft respectively (Fig. 11). The mean top height also decreases with deterioration in soil fertility. Association M3 is the shortest of the forest associations. It grows on low fertility soils developed on slow-weathering parent rock and the mean soil depth is only 7.7in. Pioneer forest is generally shorter than the forest which succeeds it. Association P1 is shorter than associations P2, C1, C2, and C3, which replace it and association P3 is generally shorter than its successor C4.

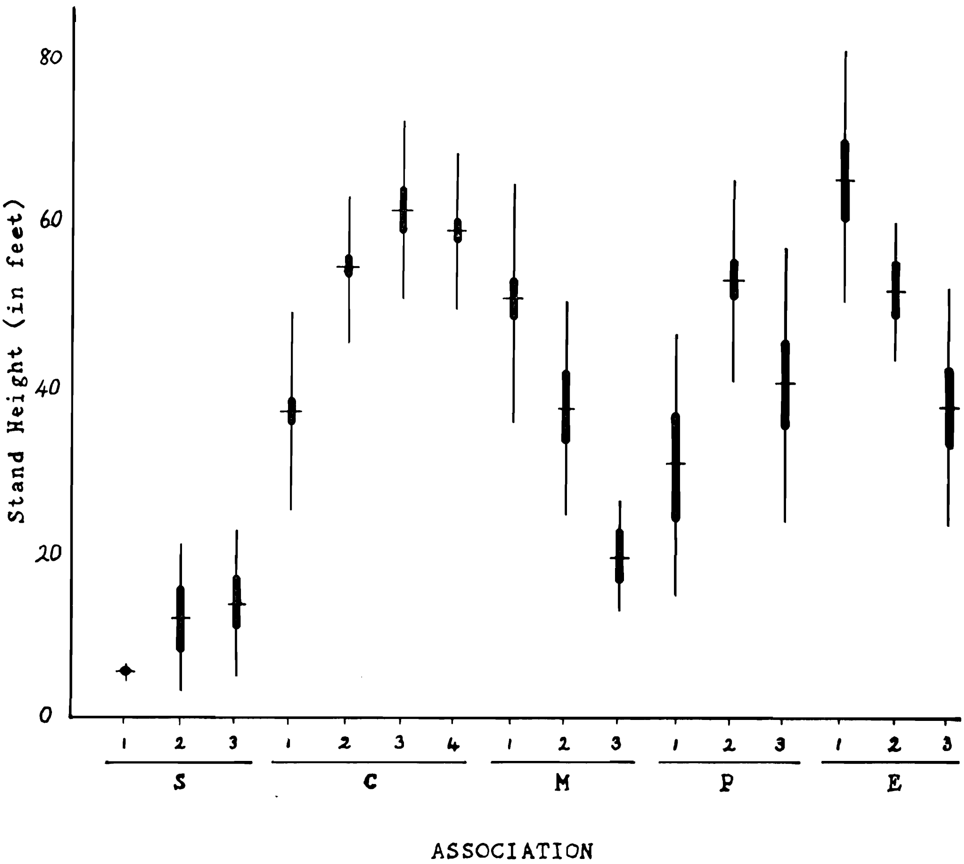

FIG. 11—Stand heights. The mean, standard error (P = 0.05) and standard deviation for each association is shown.

The complexity, or mean number of vascular plant species, for each association has been calculated on the assumption that the plot area in each case exceeds the minimal stand area (Wardle, 1970). The complexity is generally less in the east than in the west. The eastern associations, E1, E2, and E3 have means of 21, 6, and 11 species per stand respectively while the western associations which occupy similar altitudinal belts, C1, C2, and C3, have 26, 27 and 19 species respectively (Fig. 12). There is also a tendency for complexity to decrease with increase in altitude up to timber line but to increase again slightly in the sub-alpine scrub. Complexity also tends to decrease with decrease in soil fertility and to increase following development from a pioneer to a sub-climax stand.

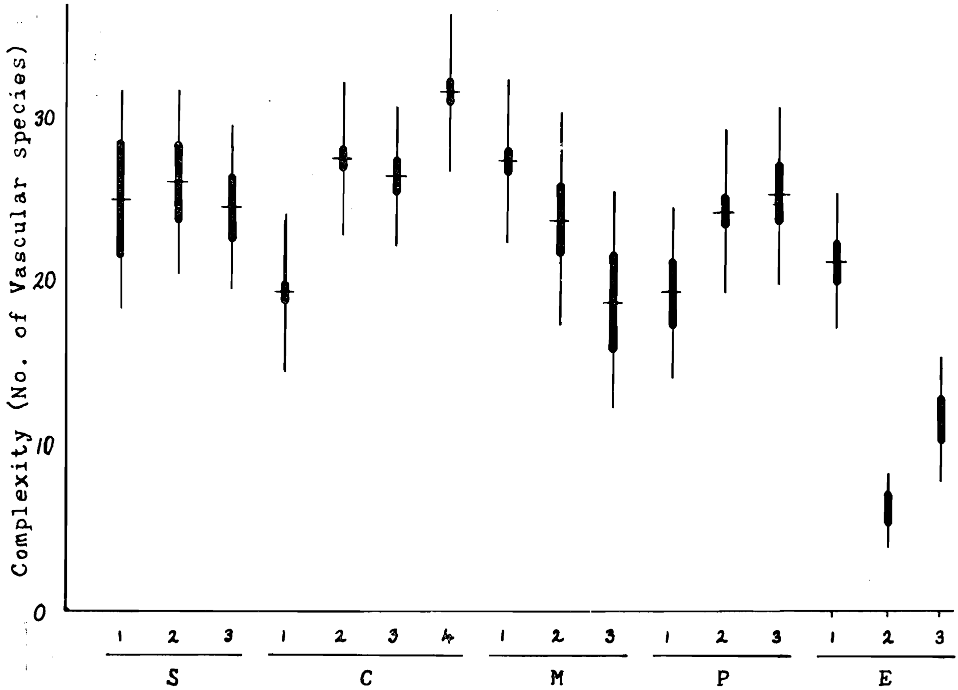

FIG. 12—Stand complexity. The mean, standard error (P = 0.05) and standard deviation for vascular plant species in each association is shown.

ANIMAL-PLANT INTER-RELATIONSHIPS

Susceptibility and trend in vegetation

(a) *Individual species*

The species which are most susceptible to browsing damage by red deer and wapiti are those with high susceptibility ratings (Table 4). Those with the highest ratings, such as fuchsia, broadleaf, putaputaweta, wineberry, lacebark, and *Asplenium bulbiferum,* show a marked regeneration gap and are expected to be elminated from many of the areas they now occupy if animal pressure is maintained at the present level. Other species, with susceptibility ratings which are lower, may tend to increase. This process of some species increasing to fill the gap resulting from the extinction of the most susceptible species is likely to be slow with tree species since most of the ones with low ratings such as miro, rimu, Hall's totara, and pink pine have slow growth rates. The understorey shrub and herb species with low ratings may increase more rapidly. There is evidence from other areas which have supported ungulate populations

TABLE 4—The susceptibility rating and frequency (in the less than 15ft tiers), of each of the major species

SHRUBS AND HERBS			TREES		
Species	SR	Freq.	Species	SR	Freq.
Asplenium bulbiferum	2.33	54	Fuchsia excorticata	2.31	83
Todea superba	1.37	149	Griselinia littoralis	2.33	476
Hedycarya arborea	1.28	34	Carpodetus serratus	1.82	132
Olearia ilicifolia	1.23	37	Aristotelia serrata	1.75	56
Polystichum vestitum	1.20	332	Hoheria glabrata	1.75	133
Aristotelia fruticosa	1.18	39	Pseudopanax simplex	1.32	516
Blechnum capense	1.15	270	Schefflera digitata	1.23	112
Astelia cockaynei	1.11	428	Pseudopanax colensoi	1.16	437
Neomyrtus pedunculata	1.10	68	Pseudopanax crassifolium	1.16	119
Hebe odora	0.98	53	Elaeocarpus hookerianus	1.09	80
Coprosma astonii	0.96	433	Pseudopanax lineare	1.06	271
Coprosma rotundifolia	0.95	36	Senecio bennettii	1.05	238
Olearia colensoi	0.95	87	Weinmannia racemosa	1.02	330
Coprosma ciliata	0.94	296	Nothofagus menziesii	1.02	606
Coprosma foetidissima	0.94	581	Nothofagus solandri	1.01	196
Myrsine divaricata	0.94	538	Melicytus ramiflorus	0.98	31
Pseudowintera colorata	0.93	428	Myrsine australis	0.97	48
Phyllocladus alpinus	0.93	142	Metrosideros umbellata	0.95	163
Coprosma colensoi	0.89	329	Dacrydium intermedium	0.93	9
Dracophyllum uniflorium	0.88	81	Podocarpus ferrugineus	0.93	99
Blechnum discolor	0.86	332	Leptospemum scoparium	0.85	14
Cyathodes juniperina	0.85	34	Dacrydium cupressinum	0.85	21
Coprosma pseudocuneata	0.85	413	Podocarpus hallii	0.83	110
Chionochloa acicularis	0.83	60	Dacrydium biforme	0.76	47
Dracophyllum menziesii	0.83	47			
Dracophyllum longifolium	0.81	124			
Coprosma lucida	0.79	72			
Cyathea smithii	0.79	186			
Chionochloa flavescens	0.78	54			
Coprosma rhamnoides	0.76	71			
Archeria traversii	0.73	311			
Pittosporum crassicaule	0.71	257			
Phormium colensoi	0.56	129			

for a longer period, such as the Grey and Taramakau catchments, that some species, particularly pepperwood, *Myrsine divaricata,* and *Pittosporum crassicaule,* may increase at a noticeable rate.

(b) *Associations*

The order of susceptibility of the associations is rather similar for the overstorey regeneration and for the understorey shrub and large fern tiers, though in each case the understorey is less susceptible (Fig. 13). The class P scrub-hardwood pioneer associations, particularly P2, and the complex silver beech association which occupies the lower mid-slopes and terraces, C3, are the most susceptible to damage from browsing, in both the overstorey and understorey tiers. The remaining complex silver beech associations; C1, C2, and C3, are moderately susceptible but the subalpine scrub, mountain beech, and eastern mountain beech-silver beech forests are reasonably tolerant.

(c) *Areas*

Block 6, which includes the Worsley, Glaisnock, and Lugar catchments, and has a high proportion of scrub-hardwood pioneer forest (Fig. 7), is the area most susceptible to damage from browsing by red deer and wapiti. Block 7, which includes the Murchison

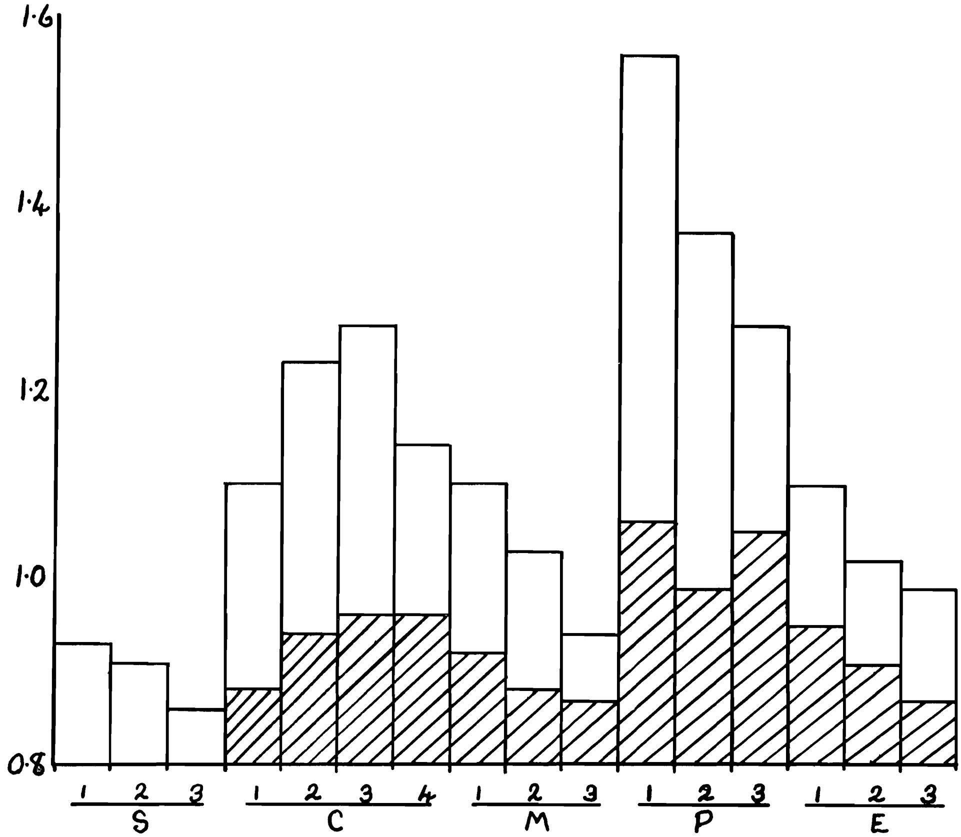

FIG. 13—Relative susceptibilities of the associations to browsing by red deer and wapiti. Understorey susceptibilities are shown hatched and overstorey open.

Range where the forest is mainly composed of mountain beech and simple silver beech associations, is the least susceptible. The remaining five blocks have rather similar susceptibilities.

Recent utilisation of the vegetation

(a) *Individual species*

Relatively few species at present form the bulk of fodder for deer and wapiti in Fiordland. The 20 species listed in Table 5, between them, provide approximately 85% of the total browse, with the first seven species: *Coprosma foetidissima, Griselinia littoralis, Pseudopanax simplex, Myrsine divaricata, Pseudopanax colensoi, Polystichum vestitum* and *Astelia cockaynei* providing about 50%. Some species such as *Myrsine divaricata, Coprosma pseudocuneata* and *Phormium colensoi* are apparently tolerant of animal browse (Table 4) but at the same time form a high percentage of the total browse (Table 5). These species must ultimately become increasingly important in providing feed for deer and wapiti if present populations of these mammals are maintained.

TABLE 5—The browse index and approximate percentage of total browse for the major fodder species. The order of preference is given. Species which produce less than 1% of total browse are not shown.

SPECIES	BROWSE INDEX	% TOTAL BROWSE
Coprosma foetidissima	606	9.33
Griselinia littoralis	536	8.25
Pseudopanax simplex	483	7.43
Myrsine divaricata	443	6.82
Pseudopanax colensoi	360	5.54
Polystichum vestitum	359	5.83
Astelia cockaynei	347	5.34
Coprosma astonii	333	5.13
Pseudopanax lineare	283	4.36
Coprosma ciliata	272	4.19
Coprosma pseudocuneata	250	3.85
Coprosma colensoi	221	3.53
Pittosporum crassicaule	199	3.06
Weinmannia racemosa	196	3.02
Nothofagus menziesii	175	2.69
Senecio bennettii	161	2.48
Todea superba	120	1.85
Pseudopanax crassifolium	82	1.26
Phormium colensoi	67	1.03
Coprosma rhamnoides	66	1.02

(b) *Associations*

The weighted percent browse frequency for each of the 12 major fodder species is given for each association, in Table 6. The order of recent utilisation of the associations derived by ranking the 16 associations in order of the weighted percent browse frequency for each of the major fodder species and then averaging the ranking order is given below:

P1 Lacebark-*Polystichum* seral forest
P2 Silver beech-*lacebark-Polystichum* seral forest
C3 Silver beech-pepperwood-*Blechnum* forest of the lower mid slopes and terraces
E3 Simple eastern mountain beech forest
E1 Eastern mountain beech-silver beech-kamahi forest
S2 Tall *Senecio* scrub
C1 High altitude silver beech-*Archeria-Senecio* forest

TABLE 6—Weighted percent browse frequencies for the twelve major fodder species in each of the 16 associations. Nil browse records are given. The index has not been calculated where there is a low frequency of a species in an association. Weighted browse frequencies of greater than 300% reflect a high utilisation of epicormic shoots.

Indicator species	ASSOCIATION															
	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Coprosma foetidissima				127	111	109	76	135	125	33		131		120		
Griselinia littoralis				333	229	722	147	286				791	78			
Pseudopanax simplex				157	140	176	80	144	133			131		159		
Myrsine divaricata				57	71	90	55	93	68			148		100		100
Pseudopanax colensoi		150	27	139	123	182	88	96	82			184		117		
Polystichum vestitum	144			73	105	153	147				230	154	85			
Astelia cockaynei			60	139	97		25	56	57			107	14			
Coprosma astonii		50		71	57	86	0	43			131	136				
Pseudopanax lineare				142	102			156	147							
Coprosma ciliata	75			76	81	108	27	89			210	120				
Coprosma pseudocuneata	44	60	14	71	56			40	57			78			40	70
Coprosma colensoi				0	61	147	56	87	47			138		80		

M1 Silver beech-rata-kamahi-mountain beech forest
C2 Silver beech-*Coprosma* forest of the upper mid slopes
M2 Mountain beech-*Phyllocladus* forest of low fertility areas
S1 Short *Hebe-Dracophyllum* scrub
C4 Kamahi-silver beech-*Cyathea* forest of the north-west lower slopes
P3 Mahoe-pate-*Cyathea* seral forest of the north-west
S3 Silver beech-*Dracophyllum* scrub
E2 Simple eastern silver beech forest
M3 Mountain beech-manuka-*Dacrydium* forest of low fertility areas

The heaviest utilisation at present is in the seral lacebark-*Polystichum* and silver beech-lacebark-*Polystichum* associations and in the silver beech-pepperwood-*Blechnum* forest of the lower mid slopes and terraces. The lightest utilisation is in the mountain beech-manuka-*Dacrydium* forest which occurs on low fertility areas.

(c) *Areas*

The weighted percent browse frequency for the 12 major fodder species is given for each of the 10 blocks (Fig. 7) of the Fiordland survey area in Table 7. The order of recent utilisation of the vegetation in the blocks, derived by ranking the 10 blocks in order of the browse indices for each of the major fodder species and then averaging the ranking order follows:

Area 7a — Eastern Stuart Range
4 — Charles Sound - Caswell Sound
5b — Western Murchison Range
6a — Eastern Franklin Range and Worsley Catchment
5a — Wapiti and Doon Catchment
3 — George Sound - Caswell Sound
2 — Bligh Sound - George Sound
7b — Eastern Murchison Range
6b — Glaisnock and Lugar Catchments
1 — Transit Catchment - Poison Bay - Sutherland Sound

The heaviest utilisation by red deer and wapiti is thus in the eastern Stuart Range and the Charles Sound-Caswell Sound area. The lightest utilisation is in the north-western Transit-Poison Bay-Sutherland Sound block, in the Glaisnock and Lugar Catchments and in the eastern Murchison Range. The order of ranking suggests that the utilisation of the vegetation in the western blocks, 1, 2, 3, and 4 progressively declines on moving north.

History of utilisation of the vegetation

(a) *Associations*

Twelve indicator species were chosen to represent the degree of modification which has occurred in the associations. The highly susceptible species were represented by broadleaf, lacebark, *Pseudopanax simplex,* and *Pseudopanax colensoi;* the moderately susceptible species by *Senecio bennettii,* kamahi, silver beech, and *Coprosma*

TABLE 7—Weighted percent browse frequencies for 12 major fodder species in each of the 10 sub-areas defined in Fig. 7. Nil browse records are given. The index has not been calculated where there is a low frequency of a species in a sub-area. Weighted browse frequencies of greater than 300% reflect a high utilisation of epicormic shoots.

Indicator species	Areas (as defined in Fig. 7)									
	1	2	3	4	5a	5b	6a	6b	7a	7b
Coprosma foetidissima	11	75	96	176	121	149	112	82	154	59
Griselinia littoralis	17	129	346	375	600			322		
Pseudopanax simplex	10	112	97	160	143	188	170	77	222	103
Myrsine divaricata	3	35	47	142	105	160	66	59	147	113
Pseudopanax colensoi	16	127	73	104	64	122	232	126	258	100
Polystichum vestitum	11	100	180	187	79	129	127	102	157	92
Astelia cockaynei	11	87	73	166	64	50	146	15	40	47
Coprosma astonii	0	56	35	102	63	100	89	73	111	59
Pseudopanax lineare	61	83	98	188	194	221	200	53		71
Coprosma ciliata	25	35	29	215	93	87	138	69	164	116
Coprosma pseudocuneata	0	47	52	83	43	73	22	33	66	43
Coprosma colensoi	0	47	29	122	88	160	129	18		

foetidissima; and the browse tolerant species by *Myrsine divaricata,* pepperwood, *Blechnum discolor,* and *Coprosma pseudocuneata.* The calculated degree of modification for each of these species, in each of the 16 associations is shown in Table 8. Three associations which have consistently high indices for the highly susceptible species are: C1 (high altitude western silver beech forest), C3 (complex silver beech forest which occupies terraces and lower mid slopes mainly in the west), and P2 (silver beech-lacebark-*Polystichum* seral forest). The only highly susceptible indicator species represented in the lacebark-*Polystichum* seral association, P1, is lacebark. The index shown by this species suggests that the vegetation in this association has also been heavily utilised by ungulates.

The highly susceptible indicator species in associations C2, C4, and P3 which are respectively the upper mid slope and lower slope complex silver beech forests, and the mahoe-pate-*Cyathea* seral forest, have consistently low indices and therefore the vegetation in these associations has received relatively little ungulate use. The low use in C4 and P3 is probably related to the predominantly north-west distribution of these associations (Fig. 7). The low use in C2 may be due to distance from forest openings. The sub-alpine scrub associations, S1, S2, and S3 are represented by only one of the highly susceptible indicator species. The index of this species, *Pseudopanax colensoi,* and the indices of the moderately susceptible indicator species, *Senecio bennettii* and silver beech, suggest that the sub-alpine scrub associations have sustained lower animal utilisation than any of the forest associations, other than perhaps P3.

The simple mountain beech and silver beech forests of the south-east, which fall into the class E associations, are hard to compare with the other associations on account of their low complexity. Except for E1 (low altitude mountain beech-silver beech-kamahi forest) these associations do not share many indicator species with the other associations. The indices of the highly susceptible and moderately susceptible indicator species which occur in association E1 other than broadleaf, suggest that this forest has had a moderately light history of animal use. Insufficient indicator species occur in E2 and E3 (simple silver beech and simple mountain beech forests), however, to deduce the intensity of ungulate use that these two associations have had.

With continued heavy ungulate use in an association it might be expected that species with low susceptibility to browsing by ungulates may increase to fill the gap caused by the extinction of browse susceptible species. If this occurred there would probably be some indication from Table 8. There would be a relative lowering of the indices of the browse tolerant species in the associations, such as P1, P2, C1, and C4, which have been most heavily utilised. However, even though there is an indication of some species such as pepperwood and *Myrsine divaricata* increasing in other areas with a longer history of animal occupation, such as the Grey catchment, there is no measured evidence for it occurring as yet in the Fiordland survey area.

(b) *Areas*

Comparison of the intensity of past utilisation in the ten blocks (Fig. 7) of the survey area by the 12 indicator species referred to above is shown in Table 9. As with the associations, the blocks where the most susceptible species show the highest indices are regarded as the blocks where the vegetation has had the most intense history of

TABLE 8—Degree of modification calculated for 12 indicator species in each of the 16 associations. The index has not been calculated where there is a low frequency of a species in an association. High indices indicate high modification.

INDICATOR SPECIES	ASSOCIATION															
	S1	S2	S3	C1	C2	C3	C4	M1	M2	M3	P1	P2	P3	E1	E2	E3
Highly susceptible																
Griselinia littoralis	—	—	—	2.94	1.85	4.18	1.45	1.61	2.63	—	—	4.17	1.33	5.00	—	—
Hoheria glabrata	—	—	—	4.00	1.18	2.70	1.25	—	—	—	2.27	1.96	0.77	—	—	—
Pseudopanax simplex	—	—	—	1.96	1.25	1.67	1.19	1.11	1.05	1.37	—	1.43	—	1.28	—	—
Pseudopanax colensoi	1.00	1.09	1.09	1.79	1.43	1.82	1.25	1.23	1.18	1.20	—	2.17	—	1.33	—	—
Moderately susceptible																
Senecio bennettii	—	0.63	—	1.14	1.20	—	—	0.99	0.69	—	—	1.18	—	—	—	—
Weinmannia racemosa	—	—	—	—	1.01	1.35	1.03	0.95	0.95	—	—	1.25	1.03	0.93	—	—
Nothofagus menziesii	—	0.83	0.73	1.00	1.09	1.00	1.03	0.93	0.93	—	—	1.10	—	1.05	1.00	0.83
Coprosma foetidissima	—	—	—	0.95	1.06	1.28	1.07	0.99	1.09	—	—	1.28	—	1.06	—	—
Browse tolerant																
Myrsine divaricata	—	—	—	0.93	1.02	1.03	1.06	0.85	0.80	—	—	1.05	—	1.00	—	0.70
Pseudowintera colorata	—	—	—	—	0.93	0.95	0.66	0.82	—	—	—	0.87	1.00	—	—	—
Blechnum discolor	—	—	—	—	0.81	0.92	0.85	0.63	—	—	—	—	—	0.83	—	—
Coprosma pseudocuneata	0.56	0.80	0.81	0.91	0.79	—	—	0.90	0.83	—	—	0.92	—	—	—	0.70

TABLE 9—Degree of modification calculated for 12 indicator species in each of 10 sub-areas. The index has not been calculated where there is a low frequency of a species in a sub-area. High indices indicate high modification.

INDICATOR SPECIES	AREA									
	1	2	3	4	5a	5b	6a	6b	7a	7b
Highly susceptible										
Griselinia littoralis	0.93	1.37	2.78	4.55	4.34	7.69	4.00	2.78	7.69	7.69
Hoheria glabrata	0.72	1.45	1.32	5.00	1.37	2.86	1.69	1.35	—	3.85
Pseudopanax simplex	0.92	1.16	1.49	1.43	1.39	1.43	1.20	1.43	1.22	1.18
Pseudopanax colensoi	0.88	1.18	1.43	1.45	1.16	1.75	1.54	1.72	1.85	1.69
Moderately susceptible										
Senecio bennettii	0.89	0.95	1.10	1.23	1.75	0.92	0.91	0.94	1.00	1.00
Weinmannia racemosa	0.91	1.02	1.01	1.07	0.89	1.22	1.12	1.23	1.00	0.87
Nothofagus menziesii	0.90	1.08	0.95	1.06	0.96	1.00	1.05	1.08	0.93	0.92
Coprosma foetidissima	1.00	1.00	1.08	1.12	1.18	1.18	1.12	1.16	1.00	1.03
Browse tolerant										
Myrsine divaricata	1.03	0.98	1.04	0.93	0.88	0.81	0.91	0.99	1.00	0.90
Pseudowintera colorata	0.98	0.90	0.98	0.90	1.04	0.85	0.67	0.92	1.00	0.61
Blechnum discolor	0.88	0.83	0.96	0.85	0.69	0.80	0.89	0.93	0.93	0.71
Coprosma pseudocuneata	0.68	0.85	0.95	0.93	0.91	0.84	0.67	0.91	0.93	0.88

ungulate utilisation. For instance, blocks 1, 2, 3, and 4, which are located from north to south on the western side of the main divide show progressively lower indices for most of the highly susceptible and moderately susceptible indicator species. Therefore it can be assumed that animal use on the western side of the main divide has been most intense in the south, but decreases progressively to the north.

If the 10 blocks are ranked in order of the indices from Table 9 for each of the highly susceptible indicator species and the ranking order is averaged, an approximate order of intensity of past ungulate utilisation of the vegetation can be derived. The order of intensity using this method is as follows:

Area 5b — Western Murchison Range
7a — Eastern Stuart Range
4 — Charles Sound-Caswell Sound
7b — Eastern Murchison Range
6b — Glaisnock and Lugar catchments
6a — Eastern Franklin Range and Worsley catchment
3 — George Sound-Caswell Sound
5a — Wapiti and Doon catchment areas
2 — Bligh Sound-George Sound
1 — Transit Catchment-Poison Bay-Sutherland Sound

The blocks which have had the history of heaviest ungulate use are 5b, 7a, 4, and 7b, and the blocks which have had the history of lightest use are 3, 5a, 2, and 1.

Comparison of the ranking order given here, which suggests history of utilisation, with the ranking order for browse frequencies, which suggest current utilisation, indicates the blocks which are receiving relatively less use and the blocks which are receiving relatively more use than previously. The blocks which are receiving relatively more use than previously are 6a, 5a, and 2. The blocks which are receiving relatively less use than previously are 5b, 7b, and 6b.

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